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Compounding effects of human development and a natural food shortage on a black bear population along a human development-wildland interface

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ABSTRACT

Human development and climate change are two stressors that threaten numerous wildlife populations, and their combined effects are likely to be most pronounced along the human development-wildland interface where changes in both natural and anthropogenic conditions interact to affect wildlife. To better understand the compounding influence of these stressors, we investigated the effects of a climate-induced natural food shortage on the dynamics of a black bear population in the vicinity of Durango, Colorado. We integrated 4 years of DNA-based capture-mark-recapture data with GPS-based telemetry data to evaluate the combined effects of human development and the food shortage on the abundance, population growth rate, and spatial distribution of female black bears. We documented a 57% decline in female bear abundance immediately following the natural food shortage coinciding with an increase in human-caused bear mortality (e.g., vehicle collisions, harvest and lethal removals) primarily in developed areas. We also detected a change in the spatial distribution of female bears with fewer bears occurring near human development in years immediately following the food shortage, likely as a consequence of high mortality near human infrastructure during the food shortage. Given expected future increases in human development and climate-induced food shortages, we expect that bear dynamics may be increasingly influenced by human-caused mortality, which will be difficult to detect with current management practices. To ensure long-term sustainability of bear populations, we recommend that wildlife agencies invest in monitoring programs that can accurately track bear populations, incorporate non-harvest human-caused mortality into management models, and work to reduce human-caused mortality, particularly in years with natural food shortages.

1. Introduction

Human development and climate change are two important stressors threatening global biodiversity (Bellard et al., 2012; Newbold et al., 2015). Expanding human development and infrastructure affect wildlife by eliminating habitat (Theobald, 2010), fragmenting and degrading existing habitat (Riitters et al., 2009), and increasing human disturbance (Trombulak and Frissell, 2000; Hansen et al., 2005), impacts which have been shown to displace wildlife (Vogel, 1989; Sawyer et al., 2006), affect movement behavior (Hurst and Porter, 2008; Cushman and Lewis, 2010), reduce demographic rates (Hansen et al., 2005), and contribute to population declines (Sorensen et al., 2008). Climate change affects wildlife by shifting long-term averages of climatic variables (e.g., warmer overall temperatures, earlier growing season) and increasing the frequency and intensity of extreme climatic events (e.g., droughts, floods; Stocker et al., 2013), which all can have substantial effects on animal behavior (Wong and Candolin, 2015), physiology (Vázquez et al., 2015), distributions (Chen et al., 2011), and population dynamics (Koenig and Liebhold, 2016).

Recent research efforts have increasingly focused on understanding the cumulative and interactive effects of multiple stressors on wildlife populations as investigators have recognized the diverse pressures influencing animals and the potential for detrimental additive or synergistic effects (Brook et al., 2008; Mantyka-Pringle et al., 2012; Côté et al., 2016). Such interactions are likely to be particularly pronounced along the human development-wildland interface where multiple stressors can converge and have compounding impacts on wildlife populations. Animals living along the development-wildland interface

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must contend with climate change-induced stressors in the natural environment such as shifts in vegetative phenology (Post and Forchhammer, 2008; Monteith et al., 2011), altered weather patterns (Rodenhouse et al., 2009; Skagen and Adams, 2012), and increased frequency of extreme climatic events (Altwegg et al., 2006; Boersma and Rebstock, 2014), while also coping with development-induced habitat loss and fragmentation, and increased exposure to disease, pollution, and human-caused mortality (McCleery et al., 2014). For example, climate-induced declines in sea-ice have reduced foraging opportunities for some polar bears (*Ursus maritimus*), and have forced them to reside on land during summer months. While this shift to land has been associated with reduced body condition of bears, it has also been accompanied by increases in conflicts with people (Stirling and Derocher, 2012), which can result in higher rates of human-caused mortality.

The compounding effects of multiple stressors along the human development-wildland interface are particularly concerning for the American black bear (*Ursus americanus*). Black bear behavior and demography are strongly tied to climate-induced variation in natural vegetative foods (Reynolds-Hogland et al., 2007; Baruch-Mordo et al., 2014; Johnson et al., 2015), and extreme weather events can cause seasonal food shortages which have been associated with reduced reproduction (Rogers, 1987a; Elowe and Dodge, 1989) and cub survival (Rogers, 1987a; Obbard and Howe, 2008). However, such events can also elevate levels of human-bear conflicts and human-caused mortalities (Zack et al., 2003; Baruch-Mordo et al., 2014) as bears increase their use of areas of human development in search of alternative food resources (Johnson et al., 2015). Because bear populations occurring along the human development-wildland interface are subject to the combined effects of climate-induced food shortages and increased human-caused mortality (e.g., vehicle collisions, lethal management removals, and illegal kills), their populations may be particularly susceptible to decline (Lewis et al., 2014). Improving our understanding of how multiple stressors drive black bear population dynamics is critical for developing future management policies that will ensure the sustainability of bear populations as changes in climate and land use continue.

We investigated the combined effects of human development and a climate-induced natural food failure on a black bear population located near the city of Durango in southwestern Colorado. In 2012, our study area experienced a late-spring hard freeze (Peterson, 2013; Rice et al., 2014) which caused a widespread natural food shortage for black bears in the region. Johnson et al. (2015) found that, under those conditions, black bears increased their use of human development to obtain anthropogenic resources for subsidy, a behavioral shift that had unknown consequences on the bear population. Our objective was to evaluate the effects of human development and the food shortage on the population of bears in our study area based on the hypothesis that combination of those stressors would result in a substantial population decline. We integrated spatial capture-recapture data and GPS collar data to quantify the abundance, density, and population growth rate of bears before and after the food shortage along the development-wildland interface. In addition, we used our integrated spatial capture-recapture models to investigate the influence of human development on the distribution of bears on the landscape (2nd order selection; Johnson, 1980) before and after the food failure. Our analysis provides important insight about the combined effects of multiple stressors facing black bear populations along the development-wildland interface, with key implications for bear management and conservation.

2. Study area

Our study area (Fig. 1) was located in southwestern Colorado and contained the city of Durango, Colorado (37.2753°N, 107.8801°W). Durango (~18,000 residents; https://www.census.gov/quickfacts/) is surrounded by mountainous terrain ranging in elevation from 1930 to 3600 m, and is generally characterized as having mild winters and warm summers that experience monsoon rains. Vegetation in the region is dominated by ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), pinyon pine (*Pinus edulis*), juniper (*Juniperus* ssp.), mountain shrubs (*Prunus virginiana*, *Amelanchier alnifolia*, etc.) and agriculture. Agriculture in the region is primarily irrigated pasture for grazing livestock, which provides negligible food resources or cover habitat for black bears. Durango is largely surrounded by public land managed by the San Juan National Forest, Bureau of Land Management (BLM), Colorado Parks and Wildlife (CPW), La Plata County and the City of Durango.

3. Methods

3.1. General approach

To estimate population parameters for bears before and after the food shortage, we combined DNA-based spatial capture-recapture (SCR) data with GPS-telemetry based resource selection data into a single integrated spatial capture-recapture (ISCR) analysis. We limited our analysis to female black bears because we had reliable DNA and telemetry data for this segment of the population and because female demography is the key to understanding changes in the population dynamics of bears (Freedman et al., 2003; Beston, 2011). We assumed our estimates of demographic parameters applied only to the population of bears ≥ 1 year old because bears < 1 year old are unlikely to be detected by the sampling methods we used (Drewry et al., 2013; Laufenberg et al., 2016). Our approach was organized into a 2-stage analysis. In the first stage, we used GPS data and resource selection function (RSF) models to identify important 3rd-order resource selection covariates (within the home-range; Johnson, 1980) that were then used in the second stage. In the second stage, we integrated GPS and SCR data into a single model that allowed us to estimate abundance, density, detection probabilities, 3rd-order resource selection coefficients for habitat covariates identified in the first analysis, coefficients relating habitat covariates to the distribution of bears across the landscape (2nd-order selection; Johnson, 1980), and relative variable importance measures for 2nd-order habitat covariates. We obtained productivity data on important black bear foods collected during our study to characterize the natural food shortage caused by the late-spring freeze in 2012. We also obtained records of observed bear mortalities collected by CPW within our study area to use as an index of annual human-caused mortality during before and after the food shortage.

3.2. Data sources

3.2.1. Non-invasive DNA data

We used non-invasive hair sampling methods to obtain unique, multilocus genotypes for individual bears, determine individual identities, and record capture histories for capture-mark-recapture analysis (Woods et al., 1999). Each year from 2011 to 2014 we constructed an array of baited, barbed-wire enclosures (hereafter referred to as hair snares) from which we collected hair samples over multiple survey occasions. Hair snare locations were based on a regular 6×6 grid pattern with the grid-cell size set at 4×4 km. Each cell contained 1 hair snare consisting of a single strand of 4-point barbed wire stretched around and attached to ≥ 3 trees at 50 cm above ground and enclosing an area 6–10 m in diameter. We baited each hair snare with liquid scent applied to burlap hung in a tree approximately 3 m above ground and to an imitation “cache” of woody debris constructed at the center of the wire enclosure. Scent bait consisted of decomposing fish liquids, various commercial bear scents, and decomposing road-killed deer liquids. Following construction, hair snares were baited and subsequently checked every 7 days for 6 consecutive weeks each year from approximately the second week of June through the last week of July. Prior to initial baiting and after subsequent sample collections, we heat-

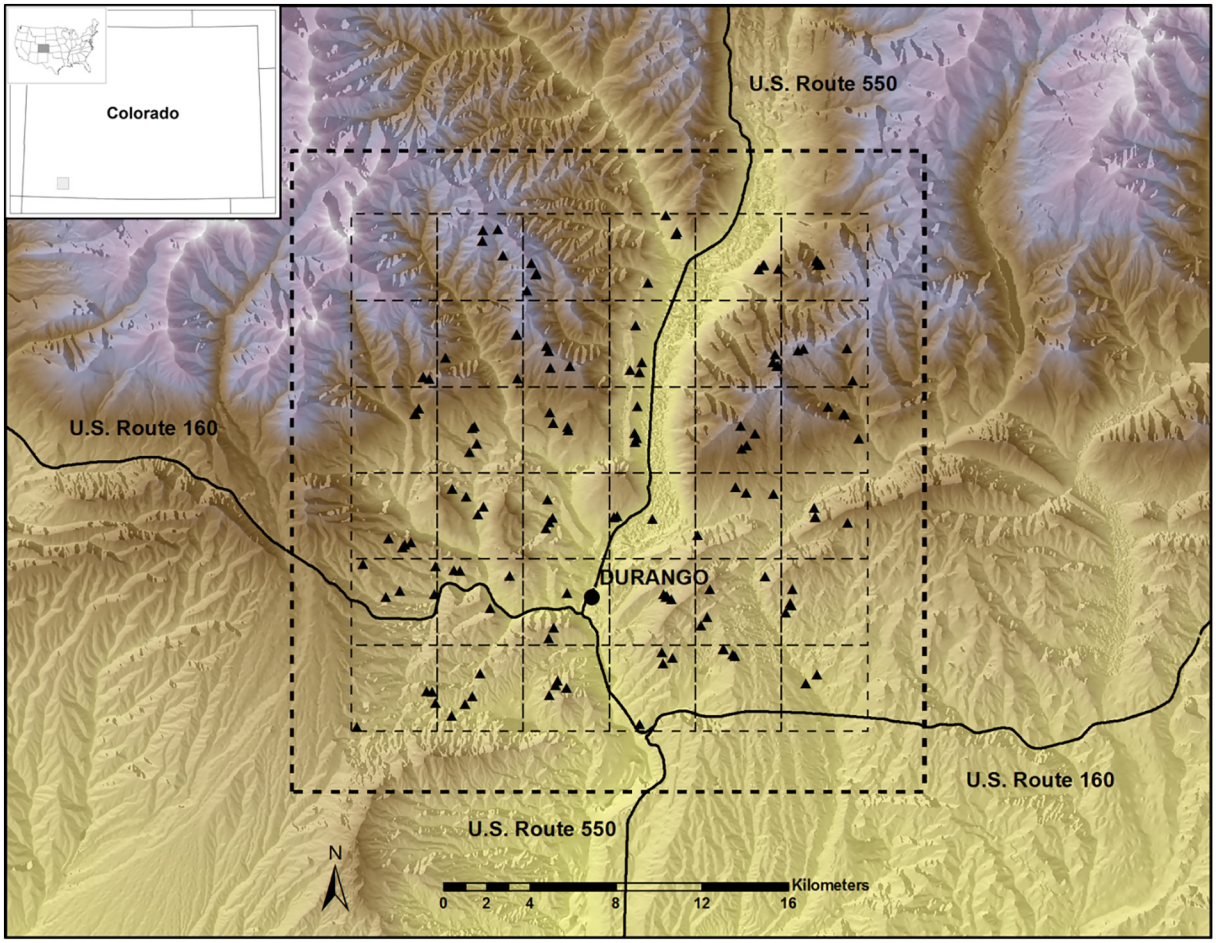

Fig. 1. Map of the study area showing the noninvasive sampling grid (thin dashed lines), hair snare locations (filled triangles) from 2011 to 2014, and state-space extent (thick dashed lines) in southwestern Colorado, USA near the city of Durango (filled circle). Major highways represented by solid lines. A single hair snare was operated per cell each year and the location of most snares changed across years resulting in multiple symbols per cell.

sterilized the barbed wire with a handheld lighter to prevent sample contamination between collection periods.

We submitted all samples to Wildlife Genetics International, Inc. (WGI; Nelson, BC, Canada) for DNA extraction and microsatellite genotyping following standard protocols (Woods et al., 1999; Paetkau, 2003; Roon et al., 2005). We selected 8 microsatellite markers (G10J, G10L, G10B, G1D, G10H, G10M, G10U, and MU59) that, when combined with a sex marker, provided sufficient power to reliably differentiate unique genotypes and identify individual black bears (Paetkau, 2003).

3.2.2. GPS-collar data

We captured black bears between May and September 2011–2014 within approximately 10 km of Durango using cage traps and Aldrich foot snares (Jonkel, 1993) following protocols described in Colorado Parks and Wildlife Animal Care and Use Protocol #01-2011. Adult female bears estimated to be ≥3 years old were immobilized and fitted with Vectronics Globstar collars (Vectronic Aerospace GmbH, Berlin). The collars were programmed to collect hourly GPS locations and were maintained during annual winter den visits so that individuals were continuously monitored until death or the collar malfunctioned. We only used GPS locations collected during the same period that hair-snare operations occurred to ensure that our SCR and GPS data sets were temporally matched for our joint analysis.

3.2.3. Mortality data

We used reports of bear mortalities opportunistically collected by CPW from 2007 to 2014 to calculate annual counts of cause-specific mortalities that occurred within our study area. We classified mortalities into 3 cause-specific categories (vehicle, harvest, and lethal management removal) and 1 "other" category (e.g., electrocution, natural, unknown). We lacked the data to correct counts for imperfect detection and, thus, consider them a relative index of different sources of mortality rather than measures of true mortality rates.

3.2.4. Natural food data

We used productivity indices of 5 hard and soft mast-producing species (Gambel oak [*Quercus gambeii*], chokecherry [*Prunus virginiana*], crabapple [*Malus* spp.], serviceberry [*Amelanchier alnifolia*], and pinyon pine [*Pinus edulis*]) important to black bears in our study area to characterize annual natural food conditions. Indices were derived from bi-weekly surveys conducted along 15 transects each year during the months of August and September (for details see Johnson et al., 2017). For each transect, the possible range of values for each species was 0 to 100 with 0 indicating no mast detected, and 100 indicating that all plants observed had abundant mast. Based on the maximum score for each mast species on each transect across the sampling period, we calculated the annual median value of mast available for each species.

3.3. Data analysis

3.3.1. RSF variable selection

We developed an RSF model of space use that was later embedded into our ISCR model to effectively scale detection probability as a

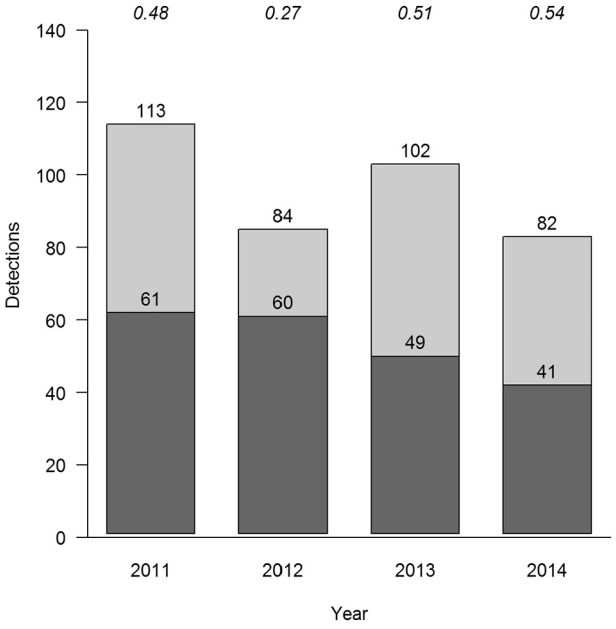

Fig. 2. Summary of DNA-based capture-mark-recapture data for female American black bears collected in southwestern Colorado, USA from 2011 to 2014. Annual number of unique bears identified are represented by dark gray columns and total number of annual detections are represented by light gray columns. Italicized values are annual proportions of unique females detected more than once.

function of distance between a hair snare and animal activity centers *and* as a function of 3rd-order resource selection. We used a standard RSF model based on a multinomial formulation of a spatial point process model for discretized space (i.e., raster data) and extended to account for resource availability as a function of distance from animal activity centers (Johnson et al., 2008; Forester et al., 2009; Royle et al., 2013). This formulation conditions on the total number of telemetry locations for each bear which is a fixed component of study design based on a known frequency for collecting locations. We assumed that missing GPS locations were randomly distributed and chose not to explicitly model them given our average fix success rate across collared female bears was high ($\bar{x} = 0.92$). Formally, our model of space use for an individual was defined as:

$$\pi(\boldsymbol{x} \mid \boldsymbol{s}) = \frac{exp(-\alpha_1 d(\boldsymbol{x},\boldsymbol{s})^2 + \boldsymbol{\alpha}\mathbf{z}(\boldsymbol{x}))}{\sum_x exp(-\alpha_1 d(\boldsymbol{x},\boldsymbol{s})^2 + \boldsymbol{\alpha}\mathbf{z}(\boldsymbol{x}))},$$

where $\pi(\boldsymbol{x}|\boldsymbol{s})$ is the probability of an animal using a raster pixel located at center coordinates $\boldsymbol{x}$ given that animal's activity center located at coordinates $\boldsymbol{s}$, $\alpha_1 = 1/(2\sigma^2)$ describes the rate of decrease in probability of use as a function of distance in terms of a scale parameter σ, $d(\boldsymbol{x},\boldsymbol{s})^2$ is the squared distance between a raster pixel and activity center, and $\boldsymbol{\alpha}$ is a vector of regression coefficients that describes the effects that covariate values $\mathbf{z}(\boldsymbol{x})$ have on the probability of use.

We fit all possible additive combinations of 14 candidate RSF covariates (i.e., percent agriculture, aspen, conifer, meadow, oak shrub, pinyon-juniper association, riparian, shrub, and subalpine, elevation, slope, terrain ruggedness, and distance to drainage; for more detailed descriptions of resource selection covariates see Supplementary material 'Spatial Covariate Descriptions') to year-specific GPS data sets. We included a quadratic term for elevation in any model that contained elevation as a main effect, as bears are known to select for intermediate elevations within the study area (Johnson et al., 2015). The final model set contained 16,383 covariate models and was balanced with respect to each covariate occurring in an equal number of models. We used a maximum likelihood approach in R (v3.2.1, R Core Team, 2015) based on code adapted from Royle et al. (2013) to fit RSF models and obtain estimates of model coefficients and variable importance. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002) and calculated model weights to estimate variable importance. For each covariate, we summed AICc model weights for all models in which the covariate of interest occurred and retained only those covariates that had cumulative weights ≥ 0.5 for subsequent analyses (Barbieri and Berger, 2004).

3.3.2. Integrated spatial capture-recapture analysis

We used SCR models extended by Royle et al. (2013) to account for the effects that heterogeneous space use has on the detection process (i.e., allowing non-circular home ranges) by explicitly modeling 3rd-order resource selection. A common approach to modeling the spatial distribution of animals in SCR models is to use a homogeneous Poisson point process model that assumes constant population density across the landscape. However, we were interested in how the distribution of female black bears across the landscape was related to habitat covariates, particularly human development, and whether those relationships changed in response to the food shortage. Therefore, we used an inhomogeneous Poisson (IP) point process model to relate habitat characteristics to black bear density (2nd-order selection). Because our habitat covariates for density were derived in discretized space (i.e., raster format), we formulated our IP model using a multinomial distribution conditional on total population size (N) for the entire state space to describe pixel-specific abundance (N_m) as a function of covariates (Royle et al., 2013). Pixel-specific abundance was linearly related to habitat covariates through the use of a log-link function and estimated regression coefficients ($\boldsymbol{\beta}$). We modeled bear density as a function of human development (DEVELOPMENT), elevation (ELEVATION), forest cover (FOREST), and stream density (STREAMS), which are similar to covariates important to predicting black bear densities in other studies (Evans et al., 2017, Sun et al., 2017; for more detailed descriptions of density covariates see Supplementary material 'Spatial Covariate Descriptions'). We fit all possible additive combinations of the 4 candidate density covariates and a constant density model (CONSTANT) to each year of data. We included a quadratic term for ELEVATION in any model that contained that covariate as a main effect. The final model set contained 16 density models and was balanced with respect to each covariate occurring in an equal number of models.

The detection model governs the observation process that produces SCR data, and includes a spatial component that scales detection probabilities as a function of space use conditional on the location of an animal's activity center. Under this formulation, space use and, thus, detection probability is modeled as a function of distance between a hair snare and an animal activity center controlled by a spatial scale parameter (σ) and as a function of resource selection coefficients ($\boldsymbol{\alpha}$). Following Royle et al. (2013), we assumed our SCR data was a random subset of use locations (e.g., GPS) "thinned" by the sampling effectiveness of the hair snare. We calculated year-specific detection probabilities, but assumed that the detection probability did not vary across occasions within a year (e.g., time effects) or was influenced by a behavioral response to bait because we used liquid lures designed to stimulate interest yet offer no food reward that would increase the likelihood of a bear revisiting a specific site. We also did not consider modeling additional sources of individual heterogeneity in detection probability because individual-level covariates were not available for bears only detected by hair snares and relatively small sample sizes precluded the use of latent heterogeneity models (e.g., finite mixtures, logit-normal).

To integrate our GPS data into our SCR analysis, we combined the likelihoods for the SCR model and the RSF model into a single analysis. Formally, we specified our ISCR model as a joint likelihood for the 2 data sets (i.e., SCR and GPS) assuming complete independence between data sets (Royle et al., 2013). Because both likelihoods contain the same model parameters governing space use (i.e., σ, $\boldsymbol{\alpha}$), information on resource selection and home range scale is shared between the two data

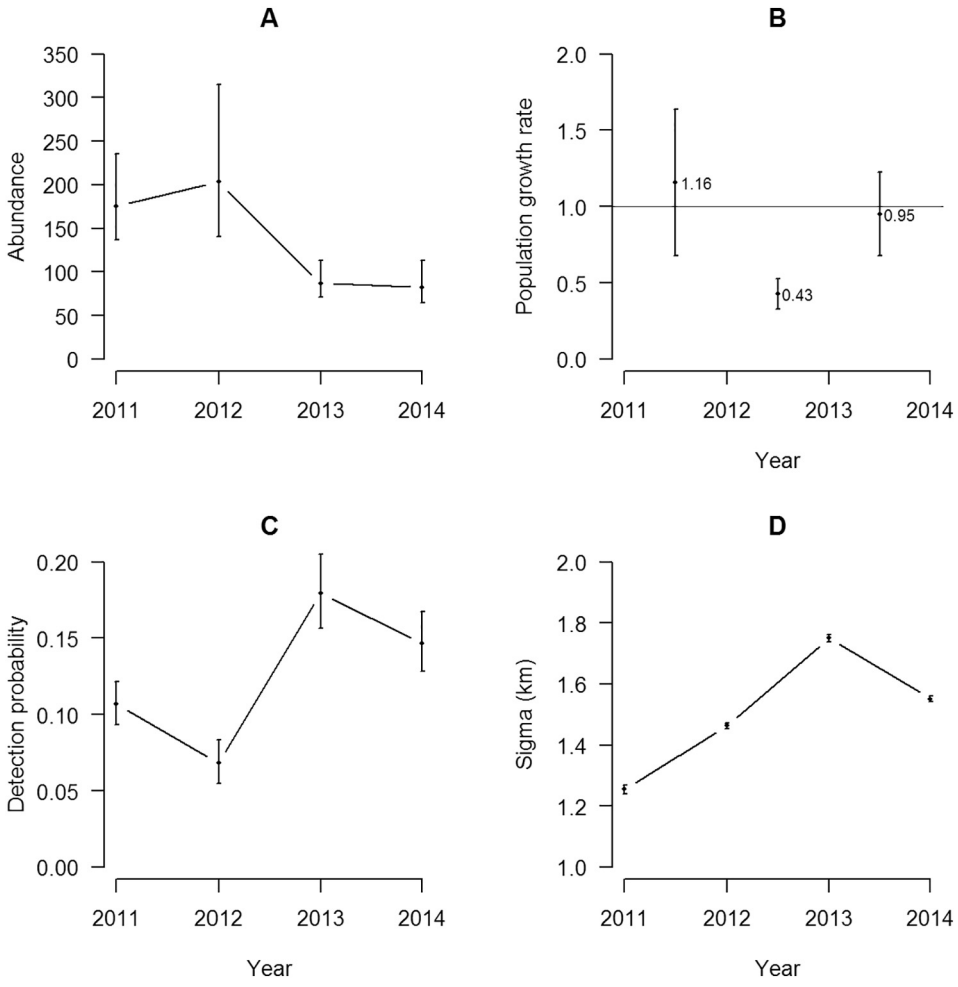

Fig. 3. Annual model-averaged parameter estimates from integrated spatial capture-recapture analyses using capture-recapture and GPS-telemetry data for female American black bears in southwestern Colorado from 2011 to 2014. Annual parameter estimates are abundance (panel A), realized population growth rate (panel B), population-level detection probability (panel C), and spatial scale of movement (panel D).

sets, allowing them to jointly estimate model parameters with improved precision. Understanding spatial patterns of resource selection, in turn, improved inferences about spatial heterogeneity in detection probabilities which then improved inferences for the point process governing estimates of abundance and spatial variation in density. Furthermore, integrating telemetry can greatly improve estimation of σ, a key detection model parameter in SCR models. As Royle et al. (2013) found, telemetry data is particularly useful for estimating σ when SCR data is sparse, which we anticipated was the case for our SCR data set.

We used a maximum likelihood approach in R based on code from Royle et al. (2013) to fit our ISCR models to each year of SCR-GPS data. We defined our state space by buffering our array of hair snares by 3 km which corresponded to a distance equivalent to $2 \times \sigma$; a distance that ensured the extent of our state space included the activity centers of all bears with access to the hair snare array (Fig. 1). The final state space had an area of 841 km^2 which we also used to define the extent of our habitat covariate rasters for modeling space use and density. We ranked models using AICc and calculated model weights for model averaging. By fitting our model set to each year of data independently, we were able to obtain year-specific model-averaged estimates of abundance and density. We derived realized population growth rates (λ) from our estimates of abundance and calculated associated sampling variances using the delta method (Powell, 2007). We derived year-specific model-averaged estimates of population-level detection probability (p) which we defined as the probability of a bear being detected at ≥ 1 hair snare in a given week. We used parametric bootstrapping to calculate sampling variances for p. Additionally, we obtained year-specific estimates of relative importance for habitat covariates in our density analysis and produced model-averaged expected-density surfaces that provided inference on how bear distribution changed within the study area over time.

4. Results

We collected 2556 hair samples between 2011 and 2014. A total of 873 were excluded due to insufficient material ($n = 840$) or being hair from other species ($n = 33$). Of the remaining 1683 samples, 423 failed to produce reliable genotypes and 2 were classified as samples containing hair from ≥ 1 bear. The final data set contained 1258 successfully genotyped samples corresponding to a genotyping success rate of 74.7%. We identified a total of 138 unique female bears across all years with year-specific counts of unique females ranging from 41 to 61 (Fig. 2). We considered all genotyped samples for an individual collected at a given trap during a given sampling occasion to represent a single detection event. Pooling samples in this fashion resulted in year-specific SCR data sets containing counts of weekly detection events (y_{ij}) indexed by individual (i) and trap (j). The total number of detections for all years was 381 with annual totals of detections ranging from 84 to 113 and annual proportion of females detected more than once ranging from 0.27 in 2012 to 0.54 in 2014 (Fig. 2). The annual average number of sampling occasions during which females were detected ranged from 1.4 (SD = 0.7) in 2012 to 2.0 (SD = 1.3) in 2013 (Supplementary

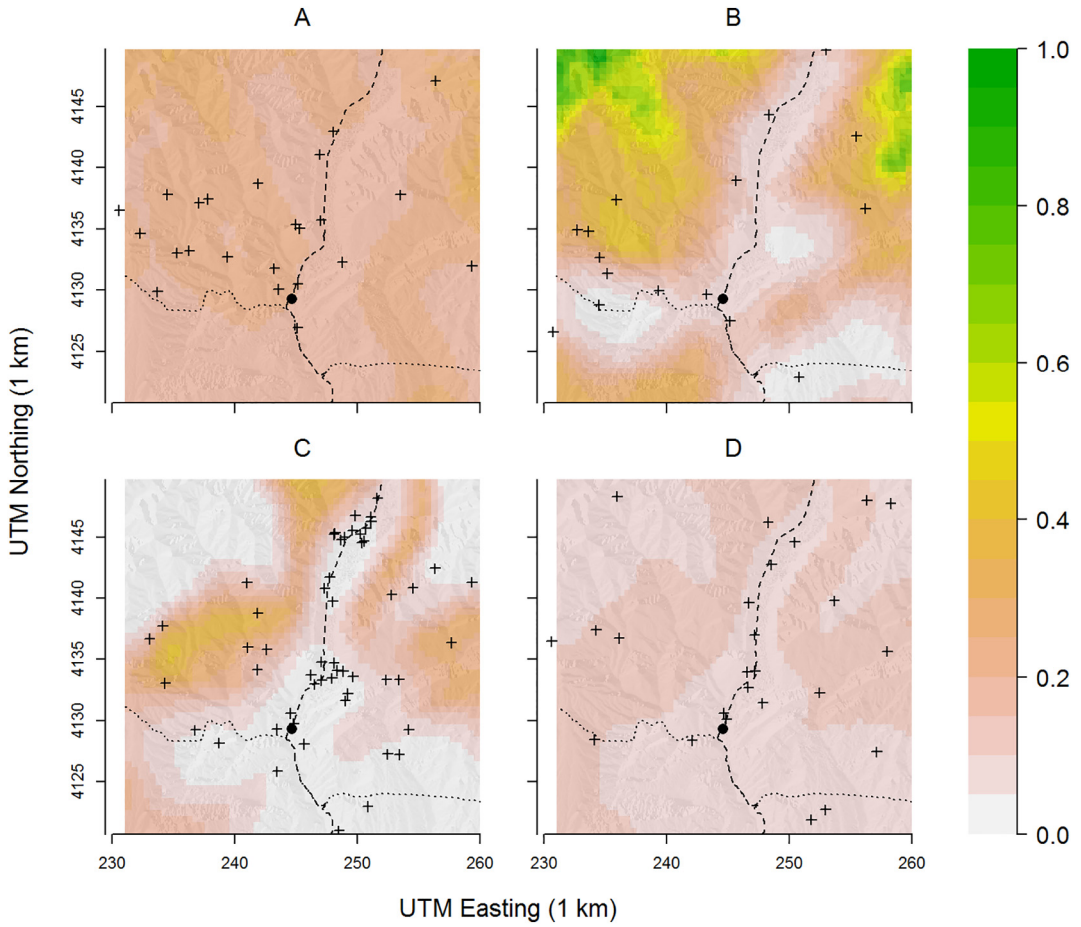

Fig. 4. Annual model-averaged predicted density (female bears/km^2) surfaces for integrated spatial capture-recapture analyses using DNA-based capture-recapture and GPS-telemetry data for female American black bears in southwestern Colorado from 2011 to 2014. Panels A–D correspond to years 2011–2014 and the city of Durango, Colorado is represented by the filled circle. Locations of reported mortalities that occurred during the 12 months prior to each year of hair sample collection (e.g., 9 June 2012 to 9 June 2013 for panel C) represented by + symbols. U.S. Route 550 and U.S. Route 160 represented by dashed and dotted lines, respectively.

material Table S1) and the annual average number of hair snares at which females were detected was 1.10 (SD = 0.3–0.4) in 2011, 2012, and 2014 and was 1.22 (SD = 0.55) in 2013 (Supplementary material Table S1).

We collected a total of 80,081 successful GPS locations from 45 unique female bears during annual hair-snare periods conducted from 2011 to 2014: 7451 locations in 2011 (10 bears), 23,476 in 2012 (27 bears), 22,423 in 2013 (23 bears), and 26,734 in 2014 (27 bears). The annual mean number of locations per female bear ranged from 745.1 (SD = 202.3) in 2011 to 990.1 (SD = 166.4) in 2014.

The number of RSF covariates identified as important (i.e., cumulative AICc weights > 0.50) in our first analysis stage and retained for the ISCR analysis varied across years from 13 to 15. Of the 15 possible covariates tested, distance-to-drainage was dropped in 2011, shrub and subalpine variables were dropped in 2012, and oak shrub and subalpine were dropped in 2013.

We estimated female abundance to be 175.6 (SE = 24.7) in 2011, 203.2 (SE = 43.0) in 2012, 86.7 (SE = 10.4) in 2013, and 82.4 (SE = 12.1) in 2014 (Fig. 3A, Supplementary material Table S2), exhibiting a marked population decline between 2012 and 2013 when the natural food shortage occurred. This corresponded to a rate of population change (λ) of 0.43 (SE = 0.05; Fig. 3B), which was significantly different (i.e., non-overlapping CIs) than λ estimates before and after the food shortage. Density estimates for the 841-km^2 state space followed the same temporal patterns as abundance and ranged from a high of 0.24 (SE = 0.05) female bears/km^2 in 2012 to a low of 0.10 (SE = 0.01) female bears/km^2 in 2014 (Supplementary material Table S2). Year-specific model-averaged estimates of detection probability (p) ranged from 0.07 (SE = 0.01) in 2012 to 0.18 (SE = 0.01) in 2013 (Fig. 3C, Supplementary material Table S2). Annual model-averaged estimates of the spatial scale of movement parameter (σ) ranged from 1.25 km (SE = 0.01) in 2011 to 1.75 km (SE = 0.01) in 2014 (Fig. 3D, Supplementary material Table S2).

Model selection uncertainty was high with no single model attaining an AICc weight > 0.50 in any year (Supplementary material Tables S3–S6). Constant density models were most supported in 2011 and 2014, whereas more complex models with multiple covariates were most supported in 2012 and 2013 suggesting greater heterogeneity in the spatial distribution of female bears in those years (Fig. 4). Using a cumulative weight threshold of 0.5 to classify a covariate as an important predictor of density, DEVELOPMENT and STREAMS were important in 2012 (Fig. 5) when bear density was lower in areas of denser human development and higher in areas with greater stream densities (Fig. 4), and DEVELOPMENT and ELEVATION were important in 2013 (Fig. 5) when density was also lower in developed areas and higher in mid-elevation areas (Fig. 4). In general, during all years, bear density was lower in developed areas than undeveloped areas; however, this pattern was particularly notable in 2013 when developed areas were nearly devoid of female bears (Fig. 5).

Between 2007 and 2014, we obtained 206 bear mortality records opportunistically collected within our study area. Annual total counts ranged from 11 in 2009 to 54 in 2012, the latter being a 3-fold increase over the 5-year average prior to the food shortage in 2012 ($\bar{x}$ = 20.0 [SD = 7.2]; Fig. 6). In 2012, mortalities caused by vehicle collisions

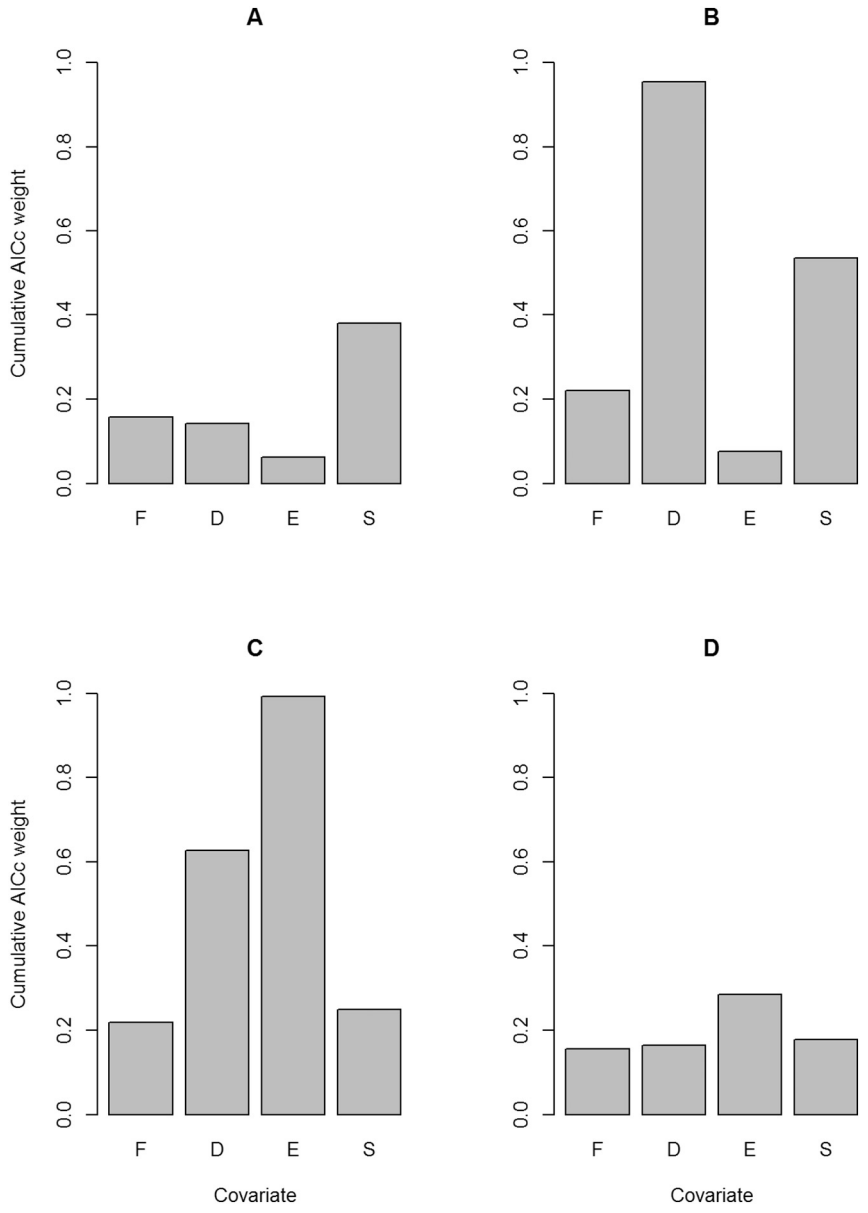

Fig. 5. Importance measures of covariates based on cumulative AICc model weights for integrated spatial capture-recapture analyses using capture-recapture and GPS-telemetry data for female American black bears in southwestern Colorado from 2011 to 2014. Panels A–D correspond to years 2011–2014 and letters F, D, E, and S correspond to FOREST, DEVELOPMENT, ELEVATION, and STREAMS covariates.

increased over 4-fold from the 5-year average of 3.4 (SD = 3.4) to 16 and 2 other human-caused sources, hunter harvest and lethal conflict removals, approximately doubled (Fig. 6).

Indices of natural foods available to bears were highly variable among years within species with species-specific CV values ranging from 0.8 to 1.4 (Fig. 7). Of the 5 mast species included in the natural food index surveys, 4 completely failed (i.e., index value = 0) to produce mast in 2012 (Fig. 7). Although no species completely failed in 2013 after the primary food shortage, productivity for 4 species remained below the mean value observed during the study indicating a possible residual climatic effect on bear foods from the previous year (Fig. 7).

5. Discussion

Our results provide evidence that human development can compound the effects of a climate-induced food shortage to significantly reduce a black bear population. Previous studies have found that food shortages are often associated with reduced recruitment in black bears (Rogers, 1987a; Elowe and Dodge, 1989; Obbard and Howe, 2008), but to our knowledge, this is the first time that such a shortage has been associated with a major decline in a contiguous black bear population; notably the most severe decline that has been documented over a 1-year period. Hellgren et al. (2005) documented a similar decline, but their study focused on a small bear population (N = 23) existing in marginal habitat. In the absence of human development, natural food shortages have been found to have limited effects on bear populations. Under such conditions, recruitment is suppressed, which has little relative influence on bear population growth, whereas adult survival is unaffected (Beck, 1991; Kasbohm et al., 1996; Clark et al., 2005), the vital rate most important in driving bear population dynamics (Freedman et al., 2003; Beston, 2011). However, bears living near human development become much more susceptible to human-caused mortality (Hostetler et al., 2009; Baruch-Mordo et al., 2014; Obbard et al., 2014) as they shift their behaviors to forage on anthropogenic foods during natural food shortages. Indeed, the ultimate cause of the increase in

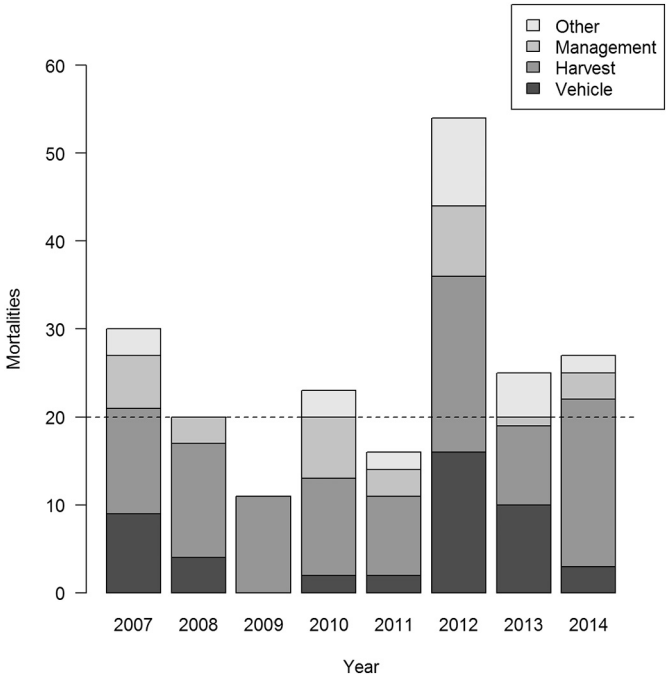

Fig. 6. Annual reported counts of 3 primary sources of human-caused mortality and all other sources combined (e.g., electrocution, natural, unknown) for male and female American black bears within the 841-km^2 study area in southwestern Colorado from 2007 to 2014. Horizontal dashed line represents the 5-year average of total counts preceding a natural food shortage in 2012.

mortalities and population decline was the food shortage of 2012, which intensified proximate factors (e.g., human-bear interactions) that led to a much greater level of human-caused mortality within our study area compared with the previous 5 years. In particular, mortalities caused by vehicle collisions considerably increased. A similar pattern was recently observed in the vicinity of Aspen, Colorado, where subadult and adult survival declined (≥26%) during poor natural forage years, largely as a consequence of bear-use of development and human-induced mortality (Baruch-Mordo et al., 2014).

The food shortage during the summer–fall period of 2012 primarily was the result of a late-spring frost event that severely reduced berry and nut production (Peterson, 2013; Rice et al., 2014). Late-spring frosts are known to cause mast crop failures (Neilson and Wullstein, 1980; Sharp and Sprague, 1967) and have been implicated in summer and fall food shortages in other bear populations (Beck, 1991; Obbard and Howe, 2008; Honda, 2013) indicating this phenomenon is not unique to our study system. Climate models predict, however, that these kinds of extreme weather events will likely become more common in the future (Karl et al., 2009), which may be problematic for bears; particularly as human development continues to expand across western landscapes. Lewis et al. (2014) used stochastic population simulation to evaluate the effects of increasing frequency of poor natural food years and various management-related removal scenarios on black bear populations. They found that a bear population could be sustained in scenarios with greater frequency of food failures if management removals were minimal, but would decline rapidly under scenarios where removals were high. However, the simulated demographic rates used by Lewis et al. (2014) to reflect poor food years corresponded to an asymptotic population growth rate of 0.77, a value far above the growth rate we estimated immediately following the food shortage in our study system ($\lambda = 0.43$). Although future food shortages may not be as severe as that which we observed in southwestern Colorado, we suggest that the effects of rare catastrophic events (e.g., population decline by ≥50%) be incorporated into long-term population assessments. This is especially important in the management of bears and other k-selected large carnivores, which are demographically constrained in their ability to recover from population declines induced by episodes of high human-caused mortality.

Given our modeling approach, we could not explicitly separate individual contributions of in situ mortality and emigration to the observed population decline, but suspect that the decline was primarily caused by increased mortality. Emigration for female bears is rare, as they exhibit high natal site fidelity (Beeman and Pelton, 1976; Rogers, 1987b; Jones et al., 2015), a pattern supported by our telemetry data, as only 2 of 22 GPS-collared females emigrated from the study area in response to the food shortage of 2012. Alternatively, bears may temporarily shift or expand their home ranges or undertake long-range movements in response to food shortages (Pelton, 1989; Kasbohm et al., 1998; Hellgren et al., 2005; Baruch-Mordo et al., 2014). Such changes in space-use patterns may increase use of developed areas by bears, thereby increasing exposure to human-related sources of mortality (Noyce and Garshelis, 1997; Ryan et al., 2004; Ryan et al., 2007; Obbard et al., 2014). The high concentration of mortalities we observed in developed areas in 2012 indicates such a shift in space use likely occurred in response to the food shortage. Taken collectively, the relatively low number of collared females that emigrated, the increased level of human-caused mortalities reported during the food shortage (Fig. 6), and the concentration of those mortalities in developed areas (Fig. 4) further supports our conclusion that the population decline was primarily driven by human-caused mortality rather than emigration.

We also could not disentangle in situ reproduction and immigration processes with our SCR data set. However, we believe the effects of the food shortage on reproduction can be deduced from our estimates of population growth rate between 2013 and 2014 by making a similar assumption about immigration as for emigration in that high natal site fidelity of female bears also limits immigration. Reproductive failures commonly occur in bear populations immediately following mass food shortages due to poor body condition of parous females (Eiler et al., 1989; Bridges et al., 2011). Because black bear cubs (< 1 year old) typically were too small to be detected by our hair sampling methods (Laufenberg et al., 2016), evidence of contributions from in situ recruitment processes would lag (Clark et al., 2005) and not be detected until the following year. Based on the expectation of a 1-year lag in observing a recruitment failure in our data, the net effect would be a population growth rate slightly below 1.0 for the second year following a food shortage (assuming adult survival returned to pre-food shortage levels). Our growth rate estimate from 2013 to 2014 was 0.95 (SE = 0.14) which supports the conclusion that in situ reproduction was also affected by the food shortage.

In addition to detecting a major overall population decline following the food shortage, we detected temporal changes in spatial distribution of female bears across the study area. In particular, we found that fewer female bears occurred in or near developed areas relative to undeveloped areas after the food shortage compared with density patterns prior to the food shortage (Fig. 4). We surmise that the observed changes were primarily driven by the spatial distribution and intensity of human-caused mortalities associated with roads and urban areas in those years (Fig. 4). Our inference was supported by greater estimated importance of the DEVELOPMENT covariate, a variable with a strong negative relationship with density, in 2013 following the failure. We also found that densities of female bears declined in areas of marginal habitat (e.g., high-elevation alpine) far from human development, which we presume was due to some bears leaving those areas to access food in or near areas of human development. Despite some benefits for bears of anthropogenic foods in developed environments (e.g., increased reproduction, larger body size, reduced home range; Beckmann and Berger, 2003, Beckmann and Lackey, 2008) the costs of elevated human-caused mortality can result in human development-wildland interfaces that operate as ecological traps (Nielsen et al., 2004; Beckmann and Lackey, 2008; Hostetler et al., 2009; Baruch-Mordo et al., 2014). Given the sharp decline in bear abundance estimated for

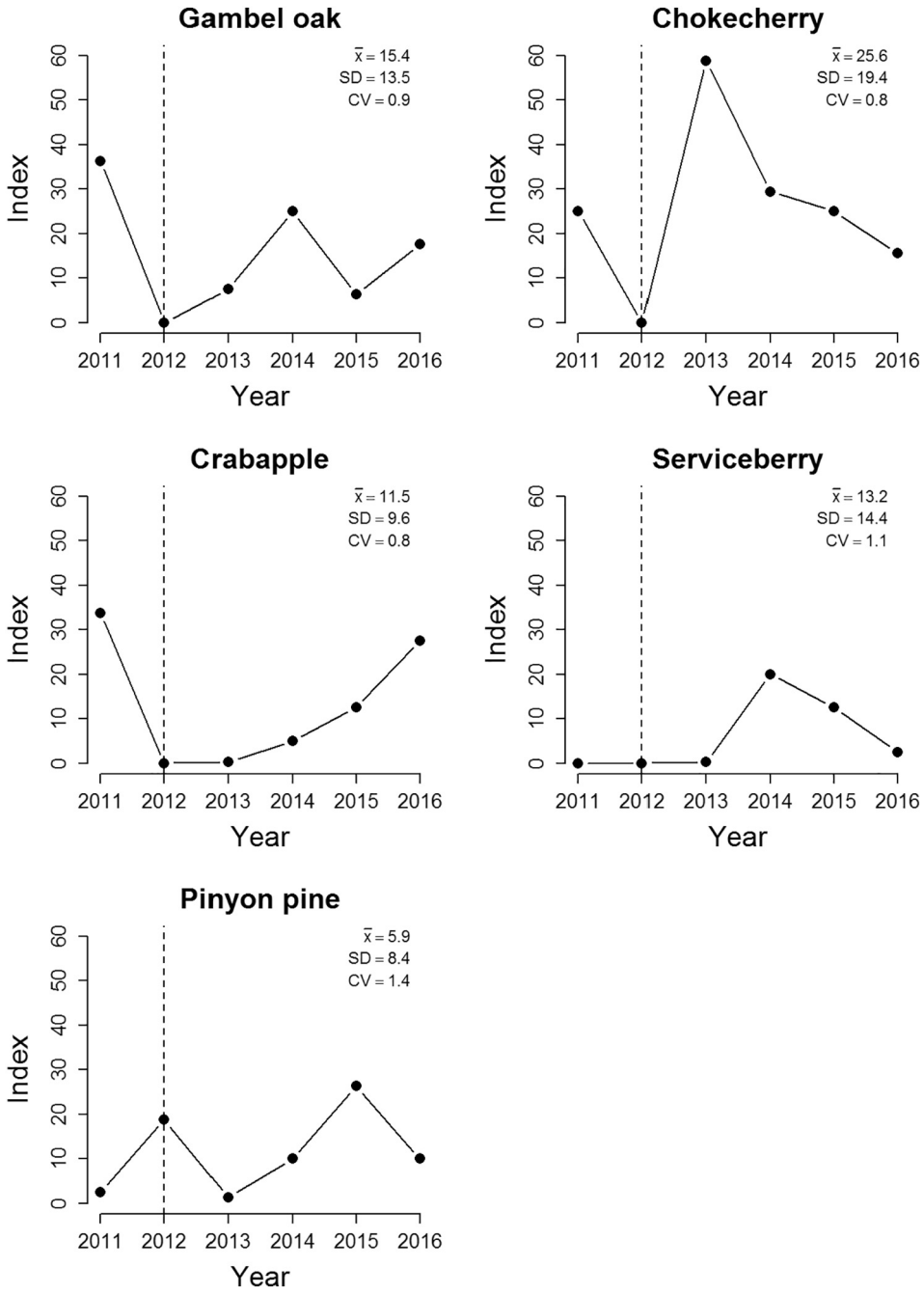

Fig. 7. Median abundance indices of 5 plants that provide hard and soft mast foods for American black bears in southwestern Colorado, USA from 2011 to 2016. The vertical dashed line indicates 2012, when there was a shortage of naturally occurring foods for black bears.

areas surrounding Durango, the overall increase in human-caused mortality following the food shortage, and the high density of those mortalities that occurred in and around development, our data would certainly support the notion that human development can serve as a population sink (Knight et al., 1988; Mattson et al., 1992; Ryan et al., 2007). This particularly is the case in poor natural food years when bears move greater distances in search for food, are attracted to town for access to anthropogenic foods, and suffer high mortality rates as a consequence (Baruch-Mordo et al., 2014). Furthermore, warmer temperatures and use of anthropogenic foods by bears have been linked to increased length of the active season which may result in even greater increases in human-caused mortality associated with developed areas thereby further exacerbating the compounding effects of predicted changes in human development and climate (Johnson et al., 2017).

Given expected increases in human development across the western U.S. (Leu et al., 2008), black bear population dynamics are likely to be increasingly influenced by non-harvest human-caused sources of mortality (e.g., vehicle collisions, lethal removals). Indeed, the annual number of non-harvest mortalities have been steadily increasing in Colorado over the past couple decades (Colorado Parks and Wildlife, 2015) as the state has seen corresponding increases in residential development, particularly in exurban and rural areas. If the frequency and severity of climate-related extreme weather events across the U.S. increases as predicted (Karl et al., 2009), the compounding effects of increasing human development and climate-induced natural food shortages may become an important determinant of long-term viability for a greater number of bear populations (Lewis et al., 2014). This shift has important implications for management agencies that typically rely

on harvest data to manage bear populations with limited information about bear population size or trend (Garshelis and Hristienko, 2006). The severe population decline detected in our study would have gone unnoticed from harvest data that are commonly collected and used to manage bears in Colorado, and was only detected due to monitoring efforts associated with an intense research project. Our results indicate management agencies may need to invest more resources into monitoring bear population trends, while accounting for non-harvest mortality rates in population models. For example, the novel integrated spatial capture-recapture approach we used could be optimized in terms of relative sampling effort for the both data types (i.e., capture-recapture and telemetry) to develop a cost-effective long-term monitoring solution.

Our results raise important questions about how management agencies can mitigate the compounding impacts of human development and natural food failures on bear populations in the future. In our system, vehicle collisions were a primary source of mortality, but effective mitigation strategies for this mortality source are unclear. In the southeastern United States, researchers have recommended the construction of highway underpasses (McCown et al., 2008; van Manen et al., 2012) but those systems differ in that bears are more continuously exposed to areas of high human density. In our system, bears are primarily drawn to development during periods of poor natural food availability. Therefore, a better strategy may be to reduce anthropogenic attractants and, thus, reduce the incentives for bears to forage within development (Baruch-Mordo et al., 2013; Johnson et al., 2018). As non-harvest human-caused mortality increases, management agencies may also need to reduce harvest and other lethal management actions to increase survival and ensure the long-term sustainability of bear populations.

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Appendix A. Supplementary materials

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.biocon.2018.05.004.

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